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IV. On the Adaptation of the Structure of the Sloths to their peculiar Mode of Life. By the Rev. WILLIAM BUCKLAND, D.D. F.R.S. F.L.S. F.G.S., and Professor of Geology and Mineralogy in the University of Oxford.

Read March 19th, 1833.

THERE are, I believe, no animals whose structure has been so generally misunderstood by naturalists, and respecting which so many errors have obtained popular acceptance, as the Sloths: they are often quoted, even by the highest authorities in comparative anatomy, as affording examples of imperfect organization, and are proverbially misrepresented, as holding the most abject place in creation, and as constructed only to lead a life of inconvenience and misery.

Cuvier (Ossemens Fossiles, vol. v. Part I. p. 72.) observes, that Buffon, after having described with eloquence, and possibly with a little exaggeration, the miserable condition in which the Sloths are placed by the organization of their bodies, says of them, "Tout en eux nous rappelle ces monstres par défaut, ces ébauches imparfaites mille fois projetées, exécutées par la nature, qui ayant à peine la faculté d'exister, n'ont dû subsister qu'un temps et ont été depuis effacées de la liste des êtres." Cuvier further states, that we find in Sloths such few relations to ordinary animals, that the general laws of existing organizations apply so little to them, and the different parts of their body seem so much at variance with the laws of co-existence which we find established throughout the rest of the animal kingdom, that we might really believe them to be the remains of another order of things, the living relics of that preceding state of nature, whose ruins we are obliged to search for in the interior of the earth, and that they have by some miracle escaped the catastrophes which destroyed the other species that were their contemporaries.

The Elephants alone, perhaps, he adds, among the Mammalia, vary in as great a degree as the Sloths from the general plan of Nature in the formation

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of this class; but the variations in the Elephant correspond with one another in such a manner as mutually to compensate any inconvenience that might arise from them, and to produce a harmonious result: "mais dans le paresseux chaque singularité d'organization semble n'avoir pour résultat que la foiblesse et l'imperfection, et les incommodités qu'elle apporte à l'animal ne sont compensées par aucun avantage." (*Cuvier, Ossemens Fossiles*, vol. v. Part I. p. 73.) He then proceeds to consider the Sloths, with respect to their peculiarities of organization, as producing slowness and debility.

The skeleton of the *Bradypus triductylus*, or Ai, as represented Pl. 4. *Cuv. Oss. Foss.* vol. v. Part II. affords proportions extremely anomalous and apparently defective; the arm and fore-arm taken together are almost double the length of the thigh and leg, so that when the animal goes on all-fours, he is obliged to drag himself upon his elbows; and if he attempted to stand erect upon his hind-feet, the entire fore-foot would still rest upon the ground: but the Ai never can stand upright, because his hind-feet are so ill articulated for walking, that they are unable to support the body in such a position; the pelvis also is so broad, and its cotyloid cavities, or sockets receiving the head of the thigh-bone, are so set back, that the thighs are kept at a distance, strutting outwards, and the knees can never approach one another. The length of the fore-legs embarrasses the animal in its attempts to walk, and its forward movements on the ground are made by fixing its claws on an object, and then dragging its body up to it.

In the above descriptions, which are almost literally translated, the learned author seems to view the structure of this animal, as Buffon had done before him, in relation only to its defects, as ill adapted to the ordinary movement of quadrupeds in walking upon the ground : had he considered its peculiarities in relation to their perfections, with reference to the habit of the animal, living constantly upon trees, and coming to the ground only for the purpose of passing from one tree to another, in those rare cases where it cannot pass from tree to tree without descending, the consideration of this habit would at once have explained all the apparent incongruities of structure; and every organ which appears so anomalous and ill adapted for walking upon the ground, would have been found pre-eminently fitted to supply the wants and comforts of an animal destined to spend its life upon trees.

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The extraordinary length of the arm and fore-arm, so inconvenient for moving on the earth, are of essential and obvious utility to a creature whose body is of too great weight to allow it to crawl to the extremity of the branches to collect the extreme buds and youngest leaves, which form its food: these long arms in fact perform the office of the instrument called 'lazy tongs,' whereby the creature brings food to the mouth from a distant point without any movement of the trunk. The structure of the arm, fixed to the shoulder by an universal joint admitting of rotation, and having at the elbow two kinds of articulation, which allow pronation and supination, gives to the hand a power of moving in every possible direction. The breadth of the pelvis and outward position of the thigh-bones, which are also broad and flat, the distance of the knees from one another, and curvature of the bones of the leg, admirably adapt these extremities of the animal to the purpose of clasping, and, as it were, riding upon the trunks and branches of trees : a peculiar condition of life was to be provided for, viz. that of a quadruped which was to feed, to sleep, and, in short, to dwell ntirely upon trees; for the succulent nature of its food renders it unnecessary to descend to drink; and if we look at the anomalous extremities of this animal with a view to their use as instruments of continual suspension upon trunks and branches, the hind-legs performing the double office of adhesion and progression, and the fore-legs the quadruple function of adhesion, progression, prehension and defence, we shall find each article of deviation from ordinary structure adapted to some useful function in its peculiar economy; we shall find a new system of machinery, contrived, and set together, as it were, on a new plan from old materials, (as machines of different functions may be compounded from similar wheels, every motion having relation to some well-defined and useful end,) and the result of these deviations presenting an animal structure not less perfect in reference to its state, than those slender and graceful forms of light and active quadrupeds, with which we usually, and perhaps more justly associate our ideas of perfect symmetry and beauty.

Let us now endeavour to illustrate further some of Cuvier's descriptions of the details of the skeleton of the  $A\ddot{i}$ , by considering the adaptation of each part to the habits of an animal living exclusively upon trees, and we shall not only discern no defect or imperfection, but shall find a probable final cause for each

peculiarity that occurs in almost every bone of the skeleton, and these of course corresponding with peculiar structures in the muscles and soft parts of the animal\*. Cuvier observes with respect to the articulation of the hind-feet, that it seems contrived expressly to deprive the animal of the power of using them in the act of walking; that whereas, in most animals, the articulation of the ankle with the leg is effected by a hinge more or less pliant, which permits the foot to play upon the leg upwards and downwards, in the Sloth a pointed pivot at the bottom of the *small bone only* of the leg, enters a conical cavity on the upper surface of the astragalus or chief bone of the instep, rendering it impossible for the foot to move vertically in the ordinary manner, and allowing it only to turn horizontally upon the pointed pivot : it follows further, that the sole of the foot is in the same vertical direction with the bone of the leg, so

\* Sir Anthony Carlisle, in a paper published in the Philosophical Transactions, 1800, notices a peculiarity in the arteries of the limbs of slowly moving animals. The axillary and iliac arteries which are distributed on the muscles of the upper and lower limbs, are suddenly divided at their entrance to these limbs into a number of equal-sized cylinders, which occasionally anastomose with each other, and are exclusively distributed on the muscles of the limbs, whilst the arteries of all other parts of the body divide in the usual arborescent form. He first observed this structure in the Macauco (Lenur tardigradus, Linn.), and subsequently found a similar distribution of the arteries of the limbs in two species of Sloth; in the Bradypus tridactylus he counted 42 separate cylinders on the surface of the brachial fasciculus, besides about 20 more, which were concealed within; he found 34 similar branches in the middle of the thigh. In the Bradypus didactylus, whose movements are quicker than those of the B. tridactylus, he found a similar distribution of the arteries, but to a less degree. As the effect of this subdivision of the arteries is to retard the velocity of the blood passing to the muscles of the limbs, he points out the importance of these phenomena in relation to the physiological question, "whether the slow movement of the blood sent to these muscles he a subordinate convenience to other primary causes of their slow contraction, or whether it be of itself the immediate and principal cause."

Sir Anthony Carlisle also notices the existence of an analogous arrangement of blood-vessels in the carotid artery of the Lion, and suggests, that this peculiarity may be subservient to the long-continued exertion of the muscles of his jaws whilst holding a powerful animal, such as a Horse or Buffalo, and thus enable him to retain his prey.

Kircher in his *Musurgia* states that he received a description of the Sloth from Father Torus, Provincial of the Jesuits in America, who had animals of this kind in his possession, and made many experiments in relation to their nature and qualities. He put a long pole under the feet of one, which it seized upon very firmly, and would not let go again : the animal thus voluntarily suspended was placed between two beams along with the pole, and there it remained without meat, drink or sleep forty days. At last, being taken down, they let loose a dog on it, which after a little while the Sloth seized with his feet, and held him four days, till he died of hunger. that it never can be placed flat or have a firm tread upon the ground, but if set on the earth would rest on its outer edge. Now there is not one of these peculiarities that is not admirably adapted to render complete the mechanical power of the hind-leg and foot as organs by which the animal is enabled to attach itself most firmly, and as it were with pincers and grappling-hooks, to the trunk and branches of a tree.

The unusual stiffness of the toes and fingers is another peculiarity of the Ai, not less fitted to assist its habits of constantly living and feeding upon trees; all the bones of the fingers and toes, except the claw-bones, are inclosed in an undivided skin, and can only move together; the claws alone are separate. The first joints of the fingers and toes are united to those of the metatarsus and metacarpus; the bones of the metacarpus also being consolidated with them into a single piece, which represents what in many animals are 14 small bones. In the hind-foot there is a similar union of the first joints with the bones of the metatarsus, one bone representing what in the more active animals are 17. This stiffness of the parts, which would be inconvenient to an animal moving on the ground, becomes advantageous and a source of strength to one whose constant position and occupation are almost stationary upon a tree. The claws of the Sloth are of unusual length, and form a powerful instrument of defence; with these a Sloth has been known to strangle a dog, holding him at arm's length: on trees also it is most surprisingly tenacious of its hold, and the limbs, though possessing great capability of motion, can fix themselves almost with the rigidity of iron. Mr. Burchell has seen the limbs, even just after death, continue fast clinging round the object to which they were adhering before the animal expired.

The Sloth has till very recently been supposed to present a most extraordinary deviation from the normal character of all Mammalia in the number of its cervical vertebræ; all other Mammalia, from the Giraffe and Camel, down to the Cetacea, have invariably seven, while the Sloth was considered to have nine. Mr. T. Bell\* has lately ascertained, by the dissection of two specimens of the Bradypus tridactylus, that the two lowest of these supposed cervical vertebræ are in reality dorsal, having two small and short rudimentary ribs attached to each of them, which have been hitherto overlooked in the dissec-

\* See paper read before the Zoological Society of London, August 13th, 1833.

tions of this animal\*. The unusual position, however, of these two anterior dorsal vertebræ, so far in advance of the clavicle and scapula, enables them to cooperate with the seven true cervical vertebræ in increasing the rotatory motion and flexibility of the neck. Hence the animal has the unusual power of looking backwards over its own shoulders. We see a final cause for this arrangement in the peculiar habits of the Sloth; being always engaged in the act of climbing and clinging with its face towards the trunk or branches of a tree, with its eyes also almost hidden in long hair, to defend them from insects, it could not easily see without a greater flexibility of neck than quadrupeds usually possess. Mr. Burchell has observed that this animal can in a remarkable manner and with great facility twist its head quite round, and look in the face of a person standing directly behind it, while at the same time the body and limbs remain unmoved; as the creature, thus embracing and attached to the trunk or branch of a tree can keep no look-out in front, the increased flexibility arising from the unusual disposition of these two anterior dorsal vertebræ may be considered as a compensation, enabling it to see and guard against the approach of its enemies in flank and rear, as well as to see the position of its food; the habits of the Sloth are unique among quadrupeds, and so also is this compensation. Another advantage resulting from this unusual flexibility may be to afford ease to the neck under the peculiar position which the Sloth assumes in taking its repose. In the case of an animal, great part of whose life, when not engaged in eating, is spent in sleeping on trees, an easy attitude for repose is most essential to its comfortable existence; and accordingly we find, that the auxiliary vertebræ at the base of the neck contribute to produce that flexibility of this organ which allows the head of the animal to incline forward and rest upon its bosom. Mr. Burchell observed that his captive Sloths assumed during sleep a position of perfect ease and safety on the fork of a tree, their arms embracing the trunk, their backs resting in the angle

\* Dr. Harlan, in a highly interesting and admirable memoir on the Anatomy of the Sloth, which did not come under my observation until this paper was passing through the press, states, "that in a *Bradypus tridactylus* which he dissected, the 9th cervical vertebra supported at the extremity of the transverse process an osseous rudiment of a rib, to which it is joined by cartilage:" but he does not proceed, as Mr. Bell has done, to draw from this fact the important conclusion, that the presence of rudimentary ribs causes the vertebræ to which they are attached to be dorsal and not cervical.—See Featherstonhaugh's American Journal of Geology and Natural Science, page 501, May 1832.

of a branch, and their heads reclining on their own bosom. The animal is thus rolled up nearly to the form of a ball; the entire vertical column, including the neck, assumes a nearly circular curve; and not only is the weight of the whole body maintained in an attitude of ease and safety, but the head is supported between the arms and chest, and the face lies buried deep in the long wool which covers these parts, and is thus protected during sleep from the myriads of insects that would otherwise attack it.

The teeth of the Sloth also present peculiarities which are in harmony with the other characters of the animal; there are no incisors, because the leaves are brought to the mouth, being collected from the branches by the powerful claws which terminate the hand and perform the office of incisors. Besides the four canine teeth, there are on each side four molars in the upper and three in the lower jaw. The construction of these teeth is the most simple that exists; they are composed of a cylinder of bone, encased with enamel, and hollow at the two extremities; the upper cavity being produced by the act of mastication, which wears away the softer bony substance of the interior more readily than the exterior enamel, and the lower cavity being filled with gelatinous pulp, which maintains the continual growth of the tooth; these simple teeth being employed exclusively in the mastication of buds and leaves, are fully adequate to the wants of an animal which has no need of the more complicated compound tooth of quadrupeds that feed on the ground, and masticate vegetables of a harder or more miscellaneous kind.

Should the above criticisms be correct, which I have presumed to make on almost the only passage in the works of Cuvier that I do not read with entire assent and admiration, the construction of the Sloth is not only relieved from the imputation of feebleness or imperfection, and still more from the charge of monstrosity; but adds another striking case to the endless instances of perfect mechanism and contrivance which we find pervading every organ of every creature, when viewed in relation to the office it is destined to fulfil; and affords a new exemplification of the principle, which has been so admirably illustrated by the judicious Paley, "that the animal is fitted to its state."

The views we have been taking of the anatomy and economy of the Sloth are abundantly confirmed by the observations on the habits of this animal, published by Mr. Waterton in his Wanderings in South America. "This sin-

gular animal," he observes, "is destined to be produced, to live and to die on trees; he inhabits remote and gloomy forests: from the descriptions which have been given of the Sloth, you would suspect that no naturalist had gone into the wilds to examine his haunts, and see whether Nature has committed any blunder in the formation of this extraordinary creature. As the Indians and negroes are the people who usually catch the Sloth and bring it to the white man, it is probable the erroneoust ccounts we have hitherto had of the Sloth have arisen from examining the animal in those places where Nature never intended he should be exhibited.

"Some years ago I kept a Sloth for several months: I often took him out of the house and placed him on the ground in order to have an opportunity of observing his motions; if the ground were rough, he would pull himself forwards, by means of his fore-legs, at a pretty good pace; and he invariably shaped his course towards the nearest tree; but if I put him upon a smooth and well-trodden part of the road, he appeared to be in trouble and distress: his favourite abode was the back of a chair; and often getting all his legs in a line upon the topmost part of it, he would hang there for hours together. The Sloth in its wild state spends its whole life upon trees, not upon the branches, but *under* them; he moves suspended from the branch, he rests suspended from it, and he sleeps suspended from it; hence his seemingly bungled conformation is at once accounted for. One day, crossing the Essequibo, I saw a large two-toed Sloth on the ground upon the bank; though the trees were not twenty yards from him, he could not make his way through the sand time enough to make his escape before we landed : he threw himself on his back, and defended himself with his fore-legs: I took a long stick and held it for him to hook on, and then conveyed him to a high and stately mora; he ascended with wonderful rapidity, and in about a minute he was almost at the top of the tree; he now went off in a side direction, and caught hold of the branch of a neighbouring tree; he then proceeded towards the heart of the forest."—For more full details of his very interesting account of the Sloth tribe, I must refer my readers to Waterton's Wanderings, pp. 161, 284.

I am indebted to my friend Mr. Burchell for the following account of his personal observations on the habits of the Sloth during his late travels in South America. At Santos in Brazil, in 1826, Mr. Burchell kept a tame Sloth, a

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Bradypus tridactylus, which at the end of two months pined and died; it fed exclusively on the buds and leaves of a species of Cecropia, a tree having a slender stem of thirty or forty feet long, with horizontal branches, hollow internally, and naked, except at the extremities; these trees grow only in damp places. Mr. Burchell made use of the upper part of the trunk of one of them, which is merely a hollow tube, as a case for his barometer; the Sloth ate only the young shoots and terminal buds of the unexpanded leaves, rejecting the old leaves, on the boughs which were brought to it daily; it was always perfectly silent, and its countenance and manners were most expressive of melancholy; it fed by day, and slept much; being kept in a room, it sate upright upon its short tail, embracing the legs of a chair with all its legs. When wild, it often sleeps in the fork of a tree; it travels along the branches with its body downwards. The young cling round the body of the mother : see Plate of Bradypus tridactylus, in Prince Maximilian of Neuwied's Animals of Brazil, 1823, livr. 2.

When resident at Para, near the mouth of the Amazons, Mr. Burchell also kept two full-grown Sloths and a young one of a three-toed species (not *Bradypus tridactylus*, but of nearly similar form and habits,) in a garden inclosed with strong stockades: they were kept tied up to the pillars of a verandah to prevent their escape; against these pillars they always placed themselves in an erect position, embracing the pillar with all four legs; when not tied to the verandah, they got up into trees in the garden; they slept both day and night, always fixing their arms round something or other; their food, consisting of branches, was brought to them in the verandah; they appeared extremely stupid, and would never come to the food; they would eat no leaves but those of the *Cecropia*.

They did not mount very large trees; they ascended with their breast pressing the trunk of the tree, advancing the hind-leg beyond the fore-leg. On the ground they could neither stand nor walk, but lay sprawling on their belly, and dragged, or rather warped themselves along, laying hold of a bunch of grass or a stone with their three claws, which operated like grappling-irons, or rather pincers. All these died in a month or two. In their wild state they are seldom seen, from their colour mingling with the grey foliage of the trees, and from their being so extremely quiet and slow.

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The tame Sloths never willingly remained on the ground, except to pass from one tree to another: all the movements of the animal are slow; it moves its claws or pincers slowly; in eating it chews slowly; it also climbs slowly; the moisture of the leaves it eats suffices it for drink, without descending to obtain water. None of those kept by Mr. Burchell were ever seen to drink. The full-grown animals were never heard to utter any sound, but the young one occasionally (though rarely) gave a short cry or whistling squeak of a single note.

They showed no indication of fear, and seemed to give attention only with their eyes; they took no notice of the boy that carried them often across the garden to their place in the verandah, with their long arms sprawling; the only objects of their regard were trees; they fight on their backs, and grapple their enemy to strangulation. The use of the long wool that covers the body, and even the face, seems to be to guard them from the annoyance of insects.

The following descriptions in Piso and Marcgraf's Natural History of Brazil, p. 221, are evidently the result of personal observation on the habits of the Sloth, and confirm in every respect the views we have been taking of the structure and habits of this animal.

"Animal est ignavissimum et ad incessum plane ineptum, in arboribus lentissime rependo progreditur, ibi habitat, foliis arborum vescens; nunquam bibit, vocem rarissime edit iiiii, fere ut felis junior: arctissime, quæcunque unguibus apprehendit, tenere potest. Quando scandit, caput elevatum lentissime movendo gestat. Pluviam etiam levem admodum metuit."—" Animal sine dubio vivax. Intestinis omnibus exemptis adhuc se movebat, et pedes contrahebat ut vivum solet quando pendens ad sommm se componit. A junctura pedis cum tibia tres nervi solidissimi, ad quemlibet unguem unus intensus tendit, quibus ungues incurvare et validissime se sustentare potest\*."

Does it not follow from the above comparisons of the habits of the Sloth with its form and structure, that so far from being in any respect an imperfectly constructed animal, it is fitted with admirable perfection of mechanism to its unusual habits and peculiar condition of life? It is true, that if rapid locomotion be an essential attribute of a quadruped, the Sloth will labour under

\* Pis. et Marcgr. Hist. Nat. Bras. p. 221.

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the imputation of debility; but we have seen, that agility and activity would have been superfluous to an animal that has no occasion to run or walk, and that the slow and torpid movements of its arms and claws cause no inconvenience to a creature whose food is stationary upon trees. Adhering continually to their trunks or branches, it finds in this position protection from the assaults of terrestrial quadrupeds, whilst its strength of arm and length of claws sufficiently defend it against the serpents, which are its most formidable enemies. The charge of imperfection, therefore, can with no more justice be advanced against the construction of the Sloth because its locomotive powers upon the ground are slow, than against the structure of fishes, because they are not furnished with legs.